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INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL. III

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Winter Egg Production and the Genetic Constitution of Rhode Island Reds.—Pearl, '12, found his Barred Plymouth Rocks fell into three well-defined classes in regard to winter egg production, viz., those that did not lay at all before March 1, the zero class; those that laid less than thirty eggs with a mean at about 16 eggs, the mediocre producers; and finally those that laid over thirty eggs, the high producers. Pearl has stated, however, that the existence of the two classes of birds, mediocre and high, is the important point rather than the number of eggs at which the dividing line falls, which may be below 30 eggs in some flocks and above 30 in others. Since the record of No. 5080 is that of a typical true mediocre producer; it is clear why the division point need not fall at a particular number of eggs. If, however, the numerical record of a pullet is made the only basis for a division point, it may be pointed out that the point could be shifted by differences in environment. If, on the other hand, under the same general environment one flock was found to have a different point of division from the second flock, the latter could not be considered genetically like the first. Thus far, no satisfactory division point has been found for our Rhode Island Reds, due probably to the few records of the type shown by No. 5080 (that is, to an absence of true mediocre producers) and to the great variability in age at first egg, associated with a comparatively uniform rate of production after the appearance of the first egg. While a true mediocre producer such as No. 5080 can easily be distinguished from a high producer in Barred Plymouth Rocks, it is impossible to draw a division line on the basis of the number of eggs produced where the egg production is of the sort observed in our Rhode Island Reds. (See Figs. 3 and 4.) Except in the case of a few individuals, the only evidence for the existence of two genetically distinct groups, such as Pearl found for Barred Plymouth Rocks, is in the shape of the left-hand portion of the curves of winter egg production. If the zero producers be omitted as a wholly artificial group (*cf.* Figs. 8 and 17) this evidence becomes less satisfactory, especially as the excess of numbers on this side of the curve may well be due to environmental factors, since the effect of such factors is almost always in the direction of decreased production. Moreover, in a later paragraph it is shown that the shape of these curves depends upon certain clearly recognized factors.

In order to eliminate any miscomprehension in regard to the characteristics of a mediocre producer, I have gone over the matter personally with Pearl. It appears that his Barred Plymouth Rocks, with the exception, of course, of the zero producers, begin to lay at about the same age, but lay at *widely differing rates*. My Rhode Island Reds, on the contrary, begin to lay at widely different ages, but lay at a fairly *uniform rate*. In the Barred Plymouth Rocks, therefore, there are three distinct *types* of winter records, zero producers, mediocre producers (Fig. 12, Nos. 274 and 284) and high producers (Fig. 3). The same types of records have appeared in a flock of Brown Leghorns which we have trap-nested.

In our Rhode Island Reds, records of the mediocre type are so rare that they must be referred either to some non-genetic origin, or a chance union of two heterozygotes, such as results in the appearance of an occasional recessive in a flock that characteristically has some dominant character such as rose comb. It is quite possible that while our flock of Rhode Island Reds as a whole is homozygous for high fecundity, it is not entirely so. It is possible, of course, that many of our Rhode Island Reds are genetically true mediocre producers, but that the addition of some other genetic factor has so altered the rate of production that the records can no longer be recognized as true mediocre records.

It seems clear, then, that our Rhode Island Reds fall into the class of high producers observed in Barred Plymouth Rocks, but that the great variability in maturity results in a portion of the flock giving numerical results like those of the Barred Plymouth Rocks, but which in reality are not at all equivalent biologically. It is also clear why Castle's ('15, '16) recent criticism of Pearl's theory of egg production can not be considered to be established, in so far as it concerns *winter egg production.*

Moreover, it will be desirable in the future to distinguish clearly between the two sorts of numerical results. A discussion of the bearing of a division point at 30 eggs upon the problem is given below.

It has been maintained by Pearl that winter egg production is a satisfactory basis for selection, both for itself and as an index of the annual egg production. This would be true only when there is a definite relation between winter and annual production such as he has found for Barred Plymouth Rocks. Since winter egg production forms a part of the annual egg production with which it is to be compared, it is evident that the coefficient of correlation may be expected to have a positive value of some magnitude, unless there is a definite tendency for birds that lay well in the winter to be poor layers in the summer. On this account it has seemed best to us to compare winter production with that of the same hens for the remainder of the year. The number of birds (77) available for the comparison was not large; but the calculated coefficient (.365 ± .067), while statistically significant, being six times its probable error, is too small for use in breeding operations. While there is an evident tendency for a high winter producer to be also a high producer for the rest of the year, it seems also true, as far as the 1913–14 records are concerned—those of 1915 being at this writing incompletely worked out, though of the same general order—that there is no special tendency for birds of late start to stop early rather than late. Of course it is essential that a bird lay well in the winter if she is to make a good yearly record, and in this sense the winter egg production may be of value as a measure of fecundity, but good winter production does not insure a good annual production, nor does a low winter production necessarily mean a poor annual production. It is true, however, that birds that make the very highest records must lay throughout the entire year. From the data in hand it seems probable that winter egg production of Rhode Island Reds is not as valuable a measure of the innate fecundity capacity of a bird as it is for the Barred Plymouth Rocks.

On the average, the flocks, if grouped according to the month hatched, have an annual record that differs by an amount equal to an average winter month's production, viz., 10 eggs, as shown by Table VIII. Or, to put the matter a little differently, the average egg production of pullets hatched in March, April or May is approximately the same from February 1 to November 1. We have no evidence that the early hatched birds, on the average, stop laying earlier in the fall than those hatched later.

The influence of time of hatching on a division point at thirty eggs is very marked in the Rhode Island Reds. In Table VI the egg production of pullets laying at all during the winter is divided into an over-thirty and an under-thirty class. In the former are 68.8 per cent. of the March-hatched pullets, 58.7 per cent. of the April-hatched pullets, while of the May-hatched birds there are only 26.6 per cent. The means of the over-thirty class are 63 eggs for the February-hatched pullets, 54.9 for the March, 46.3 for the April birds, while that for the May

TABLE VIII

EGG PRODUCTION OF PULLETS HATCHED IN APRIL, MAY AND JUNE, 1915; SHOWING NUMBER OF EGGS LAID PRIOR TO AND AFTER MARCH 1, ALSO PRIOR TO AND AFTER FEBRUARY 1

	Months Hatched		
	March	April	May
Number of pullets	139	140	116
Total eggs before March 1	5,780	4,470	2,253
Total eggs after March 1 to end of year	12,951	12,974	10,982
Av. number of eggs before March 1	41.6	31.9	19.4
Av. number of eggs after March 1	93.2	92.8	94.6
Grand total	18,731	17,444	13,235
Av. yearly production	134.8	124.7	114.0
Av. number of eggs for February	10.3	12.0	11.9
Av. number of eggs before February 1	31.3	19.9	7.5
Av. number of eggs after February 1 to end of year	103.5	104.8	106.5

Note.—The data above the double bar is for birds that completed the year. A part of the data below the double bar was compiled at the end of the winter and thus includes some birds that died during the summer.

birds is 40.5. The means of the under-thirty class are 18.8 for February and for the other three months approximately 16 eggs. Now, the mean for the abstract numbers 1 to 30 is 15.5, a value which is not far from the observed mean, since the value of 18.8 eggs obtained for the February birds is probably due to the small number of individuals involved. As the value of the mean for the under-thirty birds is practically alike in all cases, and as the value of the means for the over-thirty class for the various months decreases with decreasing age, it is evident that the value, 16.1, comes mainly from the relation of the abstract numbers and has little or no significance in itself. This point will be returned to shortly.

It will be noted in Table VI that the percentage of over-thirty pullets dropped very suddenly in passing from April to May. It means, I take it, that many of the May-hatched birds did not reach a winter egg production of 30 eggs or over because of the time they were hatched. Indeed, something of this sort is to be expected when a definite number of eggs is taken for a dividing line at a particular point on the calendar. If the production curve for May-hatched pullets be examined it will be noticed that there is a large percentage of pullets in the 16–20, 21–25, and 26–30 groups. If the average monthly production of about 10 eggs be added to these groups, most of them become over-thirty birds and the percentage of over-thirty birds becomes nearly the same as that for the April-hatched pullets. This is important, since it indicates that May-hatched Rhode Island Red pullets mature too late to furnish data comparable to Pearl's Barred Plymouth Rocks, for which it is stated (Pearl '15) that April- and May-hatched pullets alone give normal records.

Birds that begin to lay by January 1 and lay at the rate of 15 eggs per month would lay 30 eggs before March 1. This rate is about the lowest *continuous* production that has been noted, for birds that lay at a less rate usually lay intermittently. Pullets that lay at the rate specified and which begin sufficiently early in the season make very good winter records. In a recent paper Pearl, '15*b*, has remarked:

> Any bird laying 18 or more eggs per month in the months of November, December, January and February may certainly be regarded as a high winter producer.

The statement as written might imply that this rate is maintained throughout all four months, but, as this means 72 eggs and as the context implies, we take Pearl's statement to mean 18 eggs for any one month. At this rate a bird beginning to lay January 1 would lay 36 eggs before March 1. Since, however, the mode of the frequency curve of age at first egg falls at the 251–260 days group, and since the median also falls near this group, it means that nearly one half of a flock of pullets hatched May 1 will not begin to lay till after January 15, and therefore will lay less than 30 eggs. The slope of the curve indicates, moreover, that the upper limit of the range falls at about 311–320 days, which means that a few individuals begin to lay so late in life that they can not be expected to make normal records. Ten months from hatching time brings birds hatched the last of April into laying some time in February. Three hundred and ten days seems, moreover, to mark the approximate boundary of a group of stragglers which perhaps corresponds to Pearl's after March 1 group of producers, *i. e.*, his zero producers. This group is represented in the curve by the shoulder which begins at this point, there being of course an overlap with the larger group, beginning somewhere about 280–290 days.

The relation of the *abstract* numbers involved in the series of data relating to winter egg production is a matter of some importance. The mean of the abstract numbers from 1–30 is 15.5, or from 0–30, 15, a value that corresponds closely to the mean value of the number of eggs laid by the under-thirty class. The mean value of the numbers above 30 beginning at 31 and proceeding to some other higher number such as 50 or 80, will depend in part on the value chosen for the higher number. If 80 be chosen as the higher limiting value, then the mean of the numbers 31–80 is found to have a value of 56.2. The mean values just given hold only when the abstract numbers are taken one at a time or when they are arranged in a symmetrical fashion about the mean, as, for example, in the ratio of 1:2:3:4, etc., and back to 4:3:2:1. If the 1–30 winter egg production group represented a definite genotype one would expect a symmetrical or nearly symmetrical distribution of the concrete numbers about their mean. If, however, the numbers (abstract or concrete, as the case may be) had some other sort of arrangement—as, for example, if they formed part of a normal curve of variation—a different set of mean values would be obtained, depending upon the steepness of the slope of the curve. If, for example, the classes 1–5, etc., to 25–30 inclusive, are formed and the central values appear in the ratio of 1:1.3:1.7:2:2.3:2.7, the mean will be 18.2. On the other hand, the mean of the abstract numbers above 30 that form the remainder of the normal curve, under some circumstances may shift downwards, as, for example, when the mode of the curve is at 50 with the upper limit of the range at 90. If the observed distribution of winter egg production is mono-modal, and if its curve, base, mode and range correspond approximately to those of the curve assumed in the preceding paragraph, the mean of the numbers 1–30 will be larger than the mean (15.5) obtained from the abstract numbers in the manner chosen at the beginning of the paragraph. That is, there is a tendency for the means of the two parts of the mono-modal curve, *i. e.,* the ones derived from 1–30 and 30–90, respectively, to approach each other in value. If, however, the curve of winter egg production is a composite of two curves, *i. e.,* mediocre and high producers, then the means tend to approach those of the abstract numbers involved when distributed symmetrically.

Some doubt exists as to how our data are to be interpreted in the light of the statements in the preceding paragraph. The mean of the under-thirty group—viz., 16—while slightly higher than that of the mean for the abstract numbers—viz., 15.5—probably is not significant, though it may perhaps be taken as an indication of the existence of two genotypes. Since, however, the mean of the over-thirty group increases with increasing age and since the percentage of birds falling in the over-thirty classes increases with increasing age, it seems probable that the shape of the observed egg production curves is due to the artificial division point at March 1, while the irregularities in the curves are due to too few numbers. Since these irregularities largely disappear if the class intervals are doubled and since, if the time limits were to be extended so as to permit all birds to begin laying, it appears probable that the curve would become a symmetrical unimodal curve. Moreover, this conclusion is strengthened by the fact that the observed mean, 46.3, of the over-thirty class of the April-hatched pullets with its upper range at 77 is lower than the value (56.2) noted for the abstract numbers 31–80. For Barred Plymouth Rocks, however, the means do not rest upon the relation between the abstract numbers, but are an expression of the average production of the two types.

A comparison of the winter egg production curves obtained with the Rhode Island Reds with the similar curves for various seasons for the Barred Plymouth Rocks brings out some interesting points. These curves are shown in Figs. 14, 15, 16 and 17. In Fig. 14 the continuous line is the frequency curve for the winter egg production at the Maine Station for 1907–08, the flock reared by Pearl from the birds previously bred by Gowell for increased egg production. The line composed of short

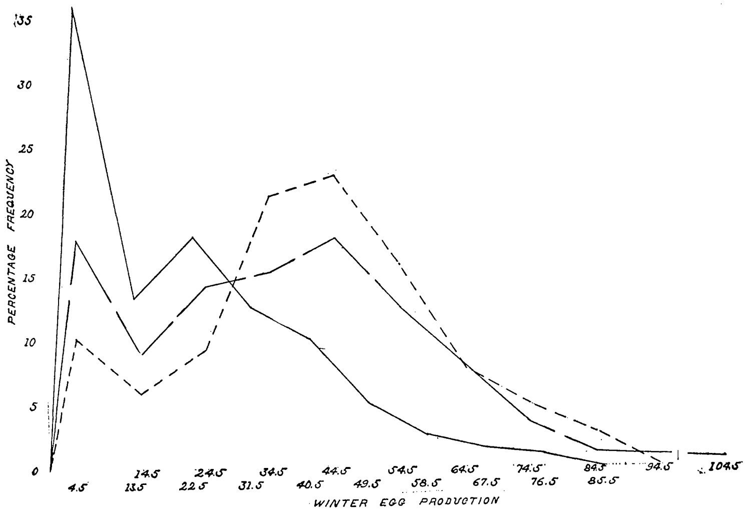

FIG. 14. Comparison of a flock of Barred Plymouth Rock pullets (Maine, 1907–08, solid line) with two flocks of Rhode Island Red pullets (Mass., 1915–16, broken line; Mass., 1913–14, dotted line) to show the difference in the shape of the winter egg production curves. For the present purpose it seemed unnecessary to regroup our data to correspond exactly to the Maine Station grouping.

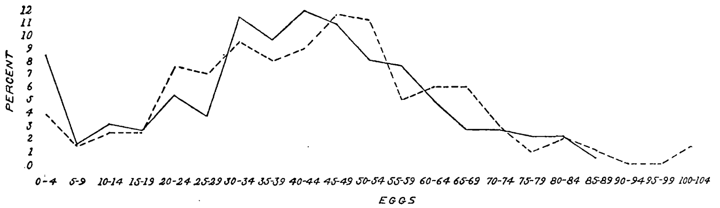

FIG. 15. Comparison of a flock of Barred Plymouth Rock pullets (Maine, 1912–13, dotted line) with a flock of Rhode Island Red pullets (Mass., 1913–14, solid line) to show the similarity in the distribution of winter egg production.

dashes is the curve of egg production for the winter of 1913–14, made by our Rhode Island Reds hatched in March and April. This flock is the first flock about which we have full data. They were the daughters of the original flock, 1912–13, as described above, and for all essential purposes were a random selection of individuals. This flock, one generation removed from its standard-bred ancestry, clearly differs from the 1907–08 flock of Pearl's in containing many more fairly high birds. The data for the 1913–14 flock, grouped in classes of 1–5 instead of 1–10, is shown by the continuous line in Fig. 15, where it is to be compared with the winter record of 199 Barred Plymouth Rocks made at the Maine Station for 1912–13.[6] The essential similarity of the two curves is self-evident. As

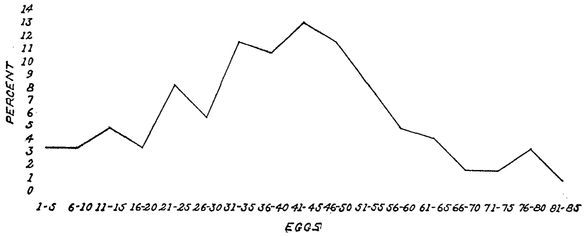

FIG. 16. Winter egg production of the Rhode Island Red pullets hatched in April, 1913. The records of these pullets have been separated from the records shown in Fig. 14 (solid line).

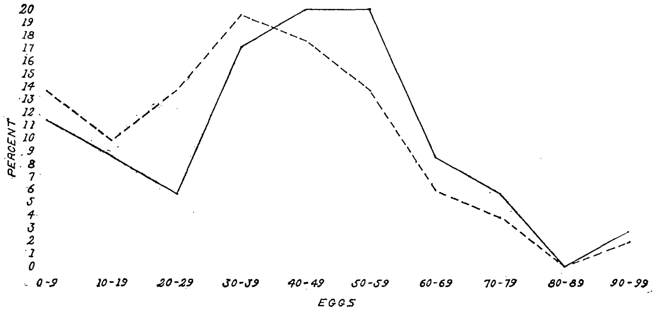

FIG. 17. Winter egg production of the flock of pullets reared in 1916 from eggs purchased of the breeder furnishing our foundation stock. The solid line represents the March hatched pullets; the broken line, the March pullets plus April hatched pullets from the same source.

[6] The data for the Barred Rocks was taken from Pearl (15*c*).

Pearl's pullets were (presumably) hatched in April and May, while ours were hatched in March and April, the curve for the April, 1913, hatched pullets alone is given in Fig. 16, which shows that the separation of the March pullets from the April pullets has not essentially altered the shape of the curve. The zero producers were omitted in order to study the shape of the curve when treating the zeros as an artificial group. This omission, however, would not alter the essential shape of the curve.

As already stated, new blood was added to our breeding pens in 1915. The egg production curve made by the pullets hatched in March and April for 1915–16 is shown by the broken line in Fig. 14. Compare also the separate curves for March- and April-hatched pullets shown in Fig. 8. Although some individual records better than any previously obtained were secured, on the whole egg production was not as good as for 1913–14, although still distinctly better than the production of the 1907–08 flock of Barred Plymouth Rocks.

The figures when grouped according to the month in which the birds were hatched show clearly the part played by this factor in determining the sort of records made. The curve for the March-hatched pullets is quite similar in appearance to the curve made by Pearl's Barred Rocks in 1913–14, except that the mode falls at a lower number of eggs. That is, the Barred Rocks contained a higher percentage of birds laying above 50 eggs than the March-hatched Rhode Island Reds. The curve, however, for the May-hatched Rhode Island Reds is much more like that of the 1907–08 curve of Barred Plymouth Rocks, while the curve for the April-hatched pullets is intermediate between the two.

It seemed a matter of some interest to determine whether our 1913–14 record was a chance record or whether it was a fair sample of the original stock. Consequently eggs were purchased from the original source and chicks reared in 1915. The first lot was hatched March 22 and all the pullets (39) that passed the test for vigor were put into a laying house in October. The egg-production curve is shown by the continuous line in Fig. 17. It bears a strong resemblance to that of the Maine Station for 1912–13 and that of our flock for 1913–14. There was in addition to the 39 pullets a smaller lot hatched April 27. The curve for both lots combined is shown by the dotted line in Fig. 17. Again the curve is essentially like the 1913–14 curve for Rhode Island Reds. The writer would be glad to study the original stock in more adequate fashion, but the amount of time, labor and equipment required are so great that the end in view did not seem to warrant the expense.

Since Pearl has not discussed the question of age at first egg from the present standpoint, the possibility must not be overlooked that the factor of maturity may play an important part in his results. In a recent paper (Pearl, '16) he states that in a good laying strain the pullets mature at five or six months on the average. Quite a different state of affairs exists in our Rhode Island Reds, where the average age is much higher, about 8½ months for the entire flock. It is clear, however, from the discussion that the factor of maturity does not influence his results to any considerable extent.

Since the two principal internal factors responsible in most cases for the number of eggs produced by a pullet during the winter are, first, the date of the first egg, and second, rate, similar sets of data may result from variability in either of the two factors. Now the date of the first egg is dependent in part on the time of year the bird is hatched, and in part on differences in maturity. The former factor is under control and can be used to eliminate differences in maturity. Rate has already been discussed in another place, but it should be noted that it may be modified by such definite factors as broodiness, or the presence or absence of cycles, as well as other physiological factors that appear to be innate but which can not be named at present. The combined effect of rate and date of first egg, or better the length of time elapsing between the first egg and March 1, is such that the same number of eggs may result from a variation in either one of these factors. If a flock of birds all begin to lay about the same time of year, but vary greatly in the rate at which they lay, a body of data superficially the same as that produced by a flock of birds laying at a fairly uniform rate but varying greatly in the time at which they begin to lay might readily result, especially if the variability of each set of factors (rate or maturity) was very much alike. Radically different sets of data would result only if the variability belonged to quite different types. The birds that make *unusually* high winter records are those that start early and lay at a good rate throughout the winter. A poor record, on the other hand, results either from a low rate combined with a long period of production (the date of first egg coming early in the fall) or from high rate and a short period of production, since the date of first egg comes late in the winter.

A late date of beginning egg production may be the result of late hatching or of delayed maturity. That is, an early-maturing bird if hatched too late may lay no more eggs than a late-maturing bird hatched early in the spring. Thus, the actual record of a bird is the result of the influence of several factors, themselves very variable, and gives much the same result as though a much larger number of factors were involved.

Pearl has spoken of two production factors, L_1 and L_2, but has not, so far as I know, assigned either to the two chief factors concerned in winter egg production, viz., rate and age at first egg, nor does the context indicate any such sense. At first sight it might seem possible that one of these factors is a factor for early maturity, the other for rate; for according to Pearl's theory both factors must be present to secure high production, since the L_1 factor in the homozygous condition does not make a high producer. So far as can be seen, there is no objection to assigning one of Pearl's two factors to rate. Some difficulties are encountered, however, in assigning maturity to either of Pearl's factors, for early-maturing birds almost invariably lay more than the required number of eggs even when their production is interrupted in some way. Since, however, the theory demands that both genetic factors be present for high production, the assignment of one factor to rate and the other to maturity can not be made.

THE SHAPE OF WINTER EGG PRODUCTION CURVES

The curves of winter egg production are clearly compound curves, probably belonging to the "S" type described by Pearl and Surface for monthly egg production in Barred Plymouth Rocks.

In the case of the winter egg production curves, it can be shown that this type of curve is due primarily to the variability in age at first egg, plus the date at which the census of the flock is taken. The curve, however, is modified somewhat by the variability in rate and by the fact that the birds were not all hatched at the same time. If a flock of birds were all hatched on the same day and all laid at some uniform rate, say an egg per day, it is clear that, on any given date between the date the first pullet commenced to lay and the date the last one began, the frequency polygon showing the number of eggs produced would consist of a zero class plus the remaining portion of the polygon, beginning at class 1 and proceeding through classes 2, 3, 4, etc., to the upper end of the range. Now the number of birds laying one egg apiece would depend upon the date chosen for the census and would be the number of birds that reached a given age on that date as shown by the curve of age at first egg. Thus, if Fig. 1 be taken as our standard, and some date early in the season be chosen for the census, say the date on which the flock becomes 186 days of age, the zero component of the egg curve would have a value of 99 per cent. and the 1-egg class a value of .6 per cent. At mid-season (256 days) the zero component would have an ordinal value of 55.3 per cent. and the 1-egg class a value of 14.3 per cent., the 11-egg class a value of 9 per cent., the 21-egg class a value of 11.4 and so on. Towards the end of the season, say at 306 days, the value of the zero class would be 13.3 per cent., and the 1-egg class would have a value of 3.1 per cent., the 11-egg class a value of 5.1 per cent., the 51-egg class a value of 14.3 and so on. At the close of the season, 366 days, the zero class disappears, while each egg class has the percentage values given in Fig. 1, beginning at the extreme right and proceeding to the left, *i. e.,* the egg curve is a mirror image of the age at first egg curve.

The first modifying factor, *i. e.,* rate, tends to flatten the theoretical egg curve by shifting individuals from one side toward the other. Thus, an individual falling in the 56 class, on the 100 per cent. rate, would fall into the 36 class at a 66⅔ rate. If a 50 per cent. rate were selected as the theoretical rate, the 66⅔ rate hen would be shoved over into the 76 class. If the date of the first egg of a sufficiently large number of pullets all hatched on the same day were plotted on a suitable calendar, a duplicate of the age at first egg curve would be obtained; but if several hatches are grouped together, *e. g.,* the four hatches occurring in any one month, it is evident that the curve plotted on the calendar would be considerably flattened and in turn would flatten out the theoretical curve of egg production as based on age at first egg.

Selection.—Pearl's success in securing increased egg production by breeding might be due to his methods of selecting the breeders, regardless of all theoretical considerations. Families that contained all high producers were selected generation after generation to propagate the high fecundity lines. Families in which true mediocre producers appeared, *i. e.,* where segregation took place, were not used in breeding for *increased* egg production. This type of selection could hardly fail to yield results, provided that egg production is inherited. Nevertheless, it is clear that fecundity is inherited in Mendelian fashion in Pearl's Barred Plymouth Rocks. However, the results obtained by Dryden at the Oregon Station show that individual selection in pedigreed lines as opposed to mass selection may result in improved egg production quite as well as by the application of Pearl's theory.

Egg production in the domestic fowl may seem at first sight to be a highly desirable character on which to study the influence of selection. It may be regarded as a unit character if one so desires, and if, by selection, this character is changed, it is clear that selection has been effective. But it is also clear that the effectiveness of such selection in this instance rests, in large measure, at least, upon the influence exerted by various modifying factors, such as broodiness or age at first egg, discussed in this paper. It is possible to study these factors individually both by themselves and also in their relation to egg production. Broodiness is known to behave like a Mendelian dominant, while Pearl has shown that the rate of production during the winter cycle is dependent on two genes, one sex-linked, the other a simple Mendelian character. We have found some evidence that the presence or absence of a winter cycle in fowls that lay at all during the winter[7] follows the Mendelian scheme. Since the influence of the various modifying factors is so clear cut, it is evident that egg production is a character wholly unsuited for studying the possibility of the modification of the germinal representatives of a character by selection. On the other hand, it is a good example of a character that varies continuously, but the continuity of whose variability can be shown to depend upon several modifying factors.

There is a point of some general interest regarding the genetic composition of any given flock. Hardy ('08) showed that the proportions in which a Mendelian character occurs tend to remain constant provided no selection is practised. Fanciers often practise a certain but indefinite amount of inbreeding. Under such circumstances there would be a tendency for the fecundity factors to remain in about the proportions in which they started. We may, therefore, expect to find ready-made flocks of high producers, true mediocre producers, or even zero producers as well as those containing the several types. Thus, the original Barred Plymouth Rocks of the Maine Station contained all three types, while the Cornish contain only true mediocre and zero producers.

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[7] The absence of a winter cycle in this instance means continuous production throughout the winter and spring, and *not* absence of egg production as in Pearl's Barred Plymouth Rocks.

In spite of the fact that we have *as yet* been unable to apply Pearl's theory of egg production bodily to our Rhode Island Reds (although it may yet be possible to use it after making some modifications) there is no question but that the ability to lay is inherited, as shown by a better egg production in some families than in others. It is clear also that some males produce offspring that on the whole make much better records than those from other males when the two groups of females with which they are mated are very similar in their winter egg production. In one instance, the difference between two sets of offspring by two males was clearly due to a difference in maturity. It seems clear, moreover, that some of the internal factors, such as broodiness and maturity, segregate independently.

SUMMARY

1. The object of the present paper is to present a survey of the problem of egg production based on the results of four years' study of egg production in Rhode Island Reds. The presentation of the data is incidental to this object.

2. On account of disturbing factors, data from two years only is presented.

3. There are two main conclusions: First: egg production in our strain of Rhode Island Reds differs in several important respects from Pearl's strain of Barred Plymouth Rocks and also from Leghorns. Second: the egg record of a hen by itself is an unsafe basis on which

to breed for definite degrees of production, for it can be shown that egg production depends on several more or less independent internal factors and that the same number of eggs may result from the action of different sets of factors. It follows, therefore, that each factor must be studied separately, both from the physiological and genetic standpoints.

4. The factors reviewed are: date of first egg, age at first egg, growth, rhythm and rate of production, including here Pearl's genetic factors L_1 and L_2, broodiness, moult, cycles, persistence of production in the autumn, and stamina.

5. Date of first egg is shown to depend on the time of hatching, the rate of growth of the young birds and some elements, at present unknown, that determine the attainment of sexual maturity. On the average it has been found that those individuals that lay early in the fall (October) lay more winter eggs than those that begin to lay later.

6. On the average, pullets that lay relatively early (6 to 7 months) in life lay more eggs than those that lay at a later period (8, 9, or more months) in life, other things being equal. The variability in age at first egg appears to be much greater for our Rhode Island Reds than for Pearl's Barred Plymouth Rocks.

7. Birds that lay rapidly, other things being equal, lay more eggs than those that lay more slowly.

8. Some birds (true mediocre producers) lay very slowly and irregularly, producing only a few eggs (1–10 or thereabouts) per month. Others (true high producers) lay much better (15–28 eggs per month).

9. The effect of the age at which the first egg is produced on winter egg production is such that numerical results, similar to those given by true mediocre producers, may result.

10. Some pullets lay continuously or nearly so, for long periods of time. Others lay relatively rapidly, but lay in cycles with a period of rest in between. These rest

periods may or may not be associated with broodiness. In a large percentage of Rhode Island Reds, a winter cycle comparable to that found in Barred Plymouth Rocks, is absent.

11. Broodiness operates to reduce egg production very materially, for the average production is about 40 per cent. higher for the period prior to the time each individual goes broody compared with average production after that time. The apparent paradox that hens with the greatest number of broody periods lay more eggs than those with fewer broody periods is due to the fact that increased production affords opportunity for more broody periods. The presence of a large amount of broodiness in our Rhode Island Reds differentiates them from the Leghorns, which lack this characteristic.

12. The appearance of a moult often stops production. A partial summer moult was noted.

13. Other things being equal, birds that lay late in the fall lay more than those that stop early.

14. Small birds mature earlier, on the average, than large ones and hence lay more winter eggs.

15. It was observed that while birds of poor stamina might make exceptionally good records, that lack of stamina tended to delay the appearance of the first egg and hence lowered the winter records.

16. It is pointed out that while the results obtained in Rhode Island Reds differ from those obtained by Pearl in Barred Plymouth Rocks in egg production, this difference must be looked upon as a real difference just as the two races differ in color.

17. Egg production is an unsatisfactory character on which to study the possible effects of selection in modifying the germ plasm, because in reality it is complex and not a simple unit character.

18. The genetic constitution of our Rhode Island Reds in respect to Pearl's L_1 and L_2 factors has not certainly been made out, but it seems probable that as a strain they fall into Pearl's class of high producers. True mediocre producers are very uncommon in this strain.

19. The relation between the means of the abstract numbers, in the series 1–30 and 30 to some higher number, and its bearing on the use of the means of egg production of two groups falling within the same limits is discussed.

20. The curves of winter egg production are shown to be compound curves.

21. A knowledge of the factors described is of importance both from the commercial and biological standpoints. As Pearl and Surface ('08) pointed out a number of years ago, the income received from each bird will depend not only on the number of eggs produced, but also on the season at which those eggs are laid. A bird that produces 100 eggs at suitable seasons may yield as much income as a bird that produces 200 eggs at less profitable seasons.

From the biological standpoint, a knowledge of the separate factors is important because what might seem at first sight to be a simple character is really extremely complex. Obviously, then, it is necessary to attack the problem from this standpoint.

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